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EXPERIMENTAL EMBRYOLOGY.

By E. A. Andrews.

The accumulation of embryological facts and their application to problems of animal morphology from the days of von Baer to the period of Balfour's text book of Comparative Embryology was carried on with ever increasing speed culminating in the present day when the revision of Balfour's work by Korschelt and Heider assumes such unexpected proportions. Though the advance of descriptive embryology has been so great, the physiological aspects of the subject have been but little cultivated, partly to be sure, from the necessary dependence of such work upon the anatomical facts that were not at first available. Now, however, when the normal development is known for all groups of animals and comparative embryology stands upon a firm basis, the application of physiological methods, the introduction of experimentation into a field promising much richer harvest than the study of adults can hope to yield, may be no longer delayed. Knowing the changes of form that ova pass through to attain the adult condition may we not both eliminate such changes as are unessential and also press nearer to the solution of more fundamental questions by varying the condition of environment and the physical state of the ovum or embryo?

Interference with the normal course of embryological phenomena was no doubt often brought about more or less unconsciously, or at least incidentally, by many of the older embryologists and remarkable results sometimes attained. Only, however, within the present decade have systematic researches been begun, definite and thought-out experiments devised and finally predictable results attained by workers in the domain of what may be called experimental embryology, though as yet the methods and the subject matter are so differently conceived by various authors and the question involved so overlaps the regions assigned to other branches of Biology that the term has at best but a vague and changing significance.

Some of the researches in this subject seem to be of such interest, though but beginnings and liable to be wrongly valued one way or the other, that a review of them here may aid in calling attention to a comparatively new line of research, one that is as yet in the limbo of pathology and thus excluded from zoological and embryological text books.

Passing over numerous experimental investigations upon the hen's egg, some of which appear to have resulted in the formation of definite, predictable monstrosities from localized interference with the embryo, we will mention only the work of Leo Gerlack[1] who finally devised a movable window, embryoscope, that allows the chick to be observed and also experimented upon from time to time while continuing to live, at least for 13 days.

With the aid of this instrument embryological problems such as the origin of the vascular system from parablast or from the primitive streak may be approached experimentally, by destroying the primitive streak for instance. By similar methods the author hopes to produce changes in embryos of several successive generations and thus strive towards the selection of important questions in heredity.

It is the frog, however, rather than the chick which has given more decided answers to physiological inquiry promising to be in its early stages what it has become as adult, an easily accessible and not so excessively equivocable an oracle.

Professor Pflüger,[2] starting from the observed facts that frogs' eggs taken from the uterus and thrown into water, float at first with variously inclined axes but after fertilization turn so that the black pole is uppermost and the white pole downward and that when cleavage takes place the first and second planes are vertical, the third horizontal was led to inquire what connection there may be between cleavage planes and gravitation.

The method of investigation was simply to remove ovarian eggs with their gelatinous capsules and fix them by their own

[1] Leo Gerlack: Ueber neuere Methoden auf dem Gebiete der experimentallen Embryologie. Biol. Centb. 7, 1888, pp. 587–605.

[2] E. Pflüger: Ueber den Einfluss der Schwerkraft auf die Theilung der Zellen. Archiv. f. Phys., 31, 1883, pp. 311–318.

viscosity upon glass plates with the white ends upward; then fertilize them artificially by sperm in so little water that the jelly does not change sufficiently to allow the egg to rotate as it normally would, but keeps it with the white side upward. In such inverted eggs cleavage takes place: moreover the first and second plane are vertical, the third often abnormal, often at right angles to the other two.

This is true when the egg is much inclined or even horizontal, that is when the egg axis, or line joining the centers of the black and the white regions, is turned out of the vertical and the first and second plane no longer intersect at this line as they normally would. Later the neural folds often appear upon the upturned white pole and throughout this pole cleaves more rapidly than the lower pole, as is the case in a normal egg with black pole uppermost.

An entirely different problem was also solved by the same method. Seventeen eggs fixed in normal positions and kept three days till the neural groove and ridges were formed, gave the direction of the median plane of the future frogs. The plane of the first cleavage furrow having been previously indicated by lines on the glass the eggs were stuck to, it was found that in twelve cases the median plane of the animal coincided with the first cleavage plane, in four it made an angle of 30°–60° and in one an angle of 90°.

To return to the effects of gravitation: it seems from a second paper[3] that normal larvæ both of *Rana esculenta* and of *Bombinator igneus* were raised from eggs held inverted as well as some larvæ partly white on the dorsal surface and not normal enough to live long.

The medullary folds, normally upon the black pole, may be made to appear upon the white pole by inclining the egg axis. The author concludes that the egg is directed by gravity so that cleavage may take place in various planes of the egg according to the position of its axis with reference to the lines of gravitation or vertical plane. Moreover, these effects are seen later, the author thinks, in the origin of the blastopore just ventral to the equator of the egg. Normally the blastopore appears just ventral to the equator and passes, so Pflüger maintained, across the white pole to the opposite side of the equatorial region. In unusual positions the blastopore also appears just beneath the horizontal equator, whatever part of the egg this equator may be in the given inclined position.

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[3] E. Pflüger: Ueber den Einfluss der Schwere auf die Theilung der Zellen und auf die Entwicklung des Embryo. Archiv. f. Phys., 32, 1883, p. 1–77. Pl. 1–2.

Pflüger came thus to regard the essential elements of an egg as having no more prearranged relationship in position to the part of the future embryo than do "snowflakes to the avalanche they may give rise to." Gravity acting to arrange the parts of an egg according to circumstances, much as snowflakes may be collected by gravity to form an avalanche, under certain circumstances.

The fundamental character of these experiments seems to be upheld by the fact presented in a third paper[4] that eggs thus held in oblique positions actually developed as far as the adult shape, quite normal toads being reared from eggs of *Bombinater igneus.*

Moreover other forces than gravitation act in the same directive fashion upon the cleavage, for Pflüger mentions his repetition of certain experiments of Rauber upon trout eggs, using eggs of both *Rana* and *Bombinator* and finding that in a rotating machine the centrifugal force controlled the appearance of cleavage planes.

Frog's eggs compressed between vertical plates of glass cleave at right angles to the plates and generally in the vertical plane also, but in exceptional cases at all angles to the vertical plane: here pressure is assumed as a sufficient determining influence.

The frog's egg is thus regarded as directly influenced by external forces and fundamentally altered in the arrangements of its constituents. The egg is like a mass of porridge with its outer part firmer and its main mass perhaps traversed by some reticulum of firmer material, but still so mobile that the heavier yolk can sink to the bottom and the less heavy remain above it, much as sediment falling in a liquid.

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[4] E. Pflüger: Ueber die Einwirkung der Schwerkraft und anderer Bedingungen auf die Richtung der Zelltheilung. Archiv. f. Phys., 34, 1884, pp. 607–616.

That this conception of the egg does not fulfil all the requirements might have been argued from the statement of Pflüger himself that the eggs experimented upon successfully, were inclined, but if placed exactly inverted with only the white pole upward, failed to develop.

It remained for Born[5] to show in what sense gravitation may be said to have anything to do with the direction of the cleavage plane and how the development of neural ridges upon what was the white pole can be brought about without there being any interchange of function between the normal neural side of the egg and the abneural white side.

Eggs fastened in an inclined position with the white showing become grey in from three quarters of an hour to two hours after fertilization. This change in appearance is due to an actual rearrangement of material beneath the firmer superficial layer of the egg, white or dark on opposite poles. The dark colored material of the egg is not confined to the surface of the dark pole, but there penetrates far towards the center in a symmetrical mass enclosing some light yolk near the center of the dark pole.

When the egg is inclined this darker material rises upward along one side of the sphere, carrying the enclosed white yolk with it, while the heavier white yolk flows down on the other side of the sphere from its forced position to a more normal one. Thus the material normally at the upper pole is brought there again, though covered over still by some superficial white yolk that remains over the white pole, now become grey.

When this rearrangement takes place at so late a stage that the nucleus is dividing as it rises, then the first plane is not necessarily vertical; gravitation acting only indirectly, while other causes determine the direction of the first cleavage plane.

Roux[6] had drawn the same inference as to the insignificance of gravity as well as light, heat, magnetism in directing the cleavage processes from rotation experiment upon frogs' eggs. Using a vertical wheel, revolving rapidly enough to produce centrifugal effect, about double that of gravitation, he found the eggs develop normally, though constantly presenting their white poles away from the centre of the wheel and being thus acted upon alternately above and below, by gravitation. Having eliminated the constant action of gravity as a directive force, he concluded it was unnecessary for the appearance of cleavage planes and assigned this to causes within the egg.

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[5] C. Born: Biologische Untersuchungen. I. Ueber den Einfluss der Schwere auf das Froschei. Archiv. f. Mik. Anat., 24, 1885, pp. 475–540. Pl. 23–24.

[6] W. Roux: Beiträge zur embryonal Entwicklungsmechanik. 2. Ueber die Entwicklung der Froscheier bei Aufhebung der richtenden Wirkung der Schwere. Bresl. Arz. Zeit., 1884, No. 6.

By numerous other contributions and complete devotion to a definite line of embryological research, this author has become as it were, the apostle of a new branch of embryology, *Entwicklungsmechanik.* Judging from the heterogenous character of the 262, 384, and 277 works for 1887, '88, '89, ranged under the above heading, as forming a separate department in Hermann and Schwalbe's *Jahresberichte* we conclude that this term is by no means synonymous with physiological or with experimental embryology, but has a much wider application, including the last as one of its subdivisions.

The first definite use of the term together with outlines of the problems to be attempted in this pre-determined field of work was made by Roux in 1885[7]. We there find *Entwicklungsmechanik* to be the science of the character and action of the combinations of energy which produce development. Also, development being the origin of observable multiplicity, there may be either read production of or merely transformation of non-observed into observable manifoldness. Epigenesis is then the actual creation of complexity: Evolution only the sensualization of latent diversities.

The key to the causal knowlege of development lies in the determination of the relative value of two possibilities: self-differentiation: interaction with the environment. Self-differentiation of a system of part is the result of the energy of the system itself. Correlative differentiation is the change of a system from loss or advent of energy from without, provided these changes are specially determined by this outside energy.

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[7] W. Roux: Beiträge zur Entwicklungsmechanik des Embryo. Zeit. f. Biologie, 21, 1885, pp. 411-524.

To determine what external forces might be at play in embryological phenomena he had thrust large pins into frog larvæ, fastening them to wax under water, in the expectation that any electrical condition of the surface would be changed by the addition of a good conductor. As some of the tadpoles developed normally he inferred the electrical state of the surface of the body was not a determining cause in the processes of growth. In this work he found certain abnormal changes in the surface cells when death took place and subsequently made use of these as a means of determining the condition of cells in early stages where there were no movements. The chief result appears, however, to have been the suggestion of a method afterwards very extensively employed.

Thus as early as 1882 he thrust needles into frogs' eggs to see if the protoplasm were arranged corresponding to the future differentiations, though recognizing the roughness of such attempts which he likens to the casting of a bomb into a factory, in hopes of drawing conclusions from the resulting changes in productivity, as to the character of damage inflicted.

On withdrawing the needle point from an egg a mass of black, or black and white yolk exudes at once and may afterwards be increased. This *extraovate* either remains connected with the wound by a narrow stalk or else separates and leaves no discoverable trace of the wounded spot. In extreme cases, one-fourth to one-fifth of the bulk of the egg may be thus lost, yet development may proceed.

Regarding the effects of wounding we find, in general, a large number of eggs develop normally, though many embryos formed are weak and small, but there are many abnormalities, some of which are like those often met with in eggs not operated upon, while others are rarely if ever found in nature. Operation at different stages produces results as follows:

Injured before cleavage had begun the eggs developed abnormally in many cases, forming larvæ with deformed heads, absent medullary folds, etc. After the first cleavage the second plane often passes through the wound and after the second cleavage one plane sometimes changed so as to pass through the wound now made. The resulting embryos often have circumscribed areas of deficient development. When injured after the equatorial plane was formed normal tadpoles were found amidst abnormal ones.

Operations after the fourth, fifth and sixth planes have appeared show that injury to the black pole produces defects in the region of the medullary folds. Blastulæ injured nineteen hours after fertilization show fewer cases of circumscribed defects. In addition it is to be noted that the exuded part of the egg may undergo by itself, a sort of cleavage resulting in the formation of a mass of numerous cells.

It thus appears that all the material of an egg is not necessary to form a normally shaped embryo: that rough mechanical disturbance of the egg material does not produce complete irregularity in the subsequent arrangements of organs: that circumscribed injuries often produce· circumscribed defects and that about the same effect results whatever stage of cleavage is injured.

The author, however, does not know why the defects are sometimes absent, nor can he produce the same defect at pleasure, in different experiments. Yet the methods of injuring definite areas of the egg is made use of in referring the cleavage planes to the axes of the subsequent embryo. Thus when eggs in the two celled stage have the needle thrust into them in the black pole, at the uppermost part of the border between black and white, the egg being naturally inclined, a circumscribed defect appears posterior to the middle of the medullary folds, whence we see that the posterior part of the medullary folds were formed over what was the white pole and the third plane divides head from tail substance.

But this question of axes and position of embryo will be dealt with later on in connection with other experiments.

The gastrula also was injured by the needle, but with conflicting results as to the circumscribed nature of the resulting defects. Deep cuts made into the gastrula yield the interesting result that each newly severed part may form its portion of the medullary fold separately. Development continued even when large tongue-shaped pieces were completely cut out. When the medullary fold region is cut lengthwise, a double-tailed monster was sometimes formed.

Larvæ with the medullary folds formed, completely cut into two, regenerate to the slight extent that an epithelial border may be formed around the rim of the wound. When cuts are made upon the ventral side the wound may heal over completely.

In all the gastrulæ and later stages the wounds led to little loss of material unless continued into the yolk mass. No subsequents defects in ectoderm were found, the wound healing over or remaining open with no formation of new ectoderm from the underlying layer. When life continued, the development was often normal though tumors were found in some cases.

Roux sees in many of the above experiments evidence for the importance of self differentiation as a principle in embryology, and also emphasizes the self regulation there observed as the most essential common character of organisms.

The interaction of the various parts of an embryo may fall under various heads not understood, but there are three chief methods insisted upon by Roux. These are functional adaptation, struggle of organs, and mechanical mass correlation.

This last factor was emphasized by Prof. His who laid stress upon the elasticity of the germ layers as an agent in bringing about folding, etc. Roux has, however, made experiments that tend to limit the application of this principle. Thus frog embryos cut into pieces showed no bending as would have resulted if there had been a tension of the surfaces. Again in a chick forty hours old the removal from yolk did not cause any gaping open of the medullary folds such as would be expected if lateral pressure had brought them about: in fact a younger embryo proceeded to form its folds even after removal, by self differentiation not by mass correlation evidently.

Then His' derivation of the the fourth ventricle from a bending of the brain, is not supported by experiments upon frogs and chicks in which, to be sure, a ventricle-like fold was produced by actual bending; but this was not in the position of the fourth ventricle and was, moreover, the result of the reaction of the living substances, not simply mass correlation.

An ingenious research into the cause determining the direction of the first cleavage plane in the egg and hence the median plane of the adult frog, as it is thought, was subsequently published in full by Roux[8] in 1887.

The method employed was simply to place eggs from the oviduct upon glass, white pole downward and allow them to adhere. Then sperm was added either by touching a cut made in the jelly with a brush moistened by sperm or else by introducing sperm through a capillary tube into one point of the jelly. Examined at frequent intervals the appearance of the cleavage planes was noted and referred to marks made upon the glass or paper under egg.

When the eggs were fastened in the normal position and were not eggs laid late in the season, when abnormalities are frequent, the following results were obtained:

Before fertilization but one axis of the embryo is indicated in the egg: the main axis of egg, that from black to white pole representing the ventro-dorsal axis of the actual embryo, which the author believes has its neural folds formed upon the white pole when held in a normal position. Yet this axis corresponds to a cephalo-caudal direction of the embryo when we consider the rearrangement of material that takes place during gastrulation. Of the infinite planes passing through this axis that one becomes the median plane of the frog which is determined by the plane of copulation of the male and female pronuclei. This plane of copulation in turn is not predetermined but may be put in any meridian by localized fertilization.

The side selected for entrance of sperm becomes the ventro-

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[8] W. Roux: Beiträge zur Entwicklungs mechanik des Embryo. IV. Die Richtungs-bestimmung der Medianebene des Froschembryo durch die Copulation richtung des Eikerns und des Spermakerns. Archiv. f. Mik. Anat., 29, 1887, pp. 157–211. Pl. X.

PLATE XV.

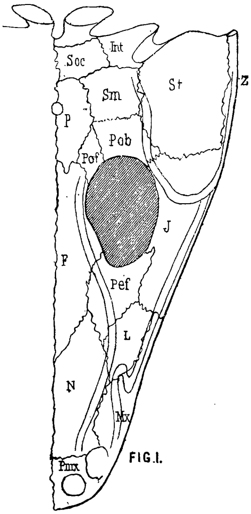

FIG. 1.

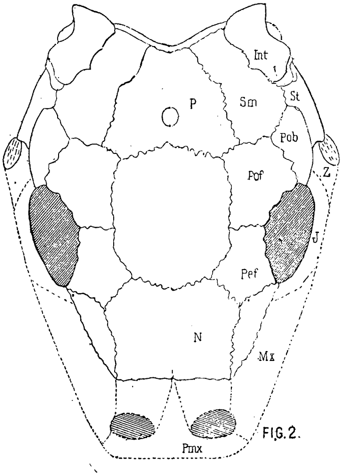

FIG. 2.

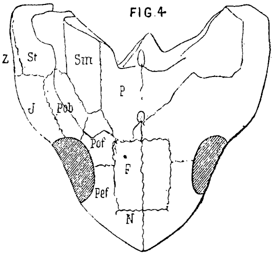

FIG. 4

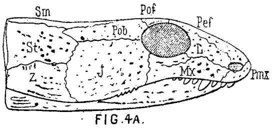

FIG. 4A.

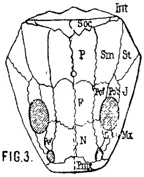

FIG. 3.

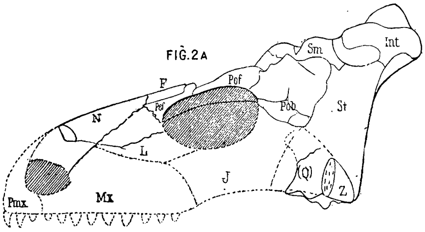

FIG. 2A

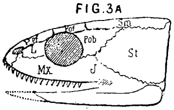

FIG. 3A

1. *Mastodonsaurus* Jaeger. 2. *Chilonyx* Cope. 3. *Pariotichus* Cope.
4. *Pantylus* Cope.

caudal and the opposite the dorso-cephalic side of the embryo. An examination of these eggs by sections shows that the course of the sperm as indicated by the trail of dark pigment left behind it is first a long radiating line from the black pole near the white rim to a layer deep within the egg in which the copulation of nuclei takes place, then a short course towards the female nucleus.

The author then points out that the cleavage in the plane of copulation ensures an easy separation of the material of both pronuclei, provided they are not intermixed in copulation, half of each being readily moved into each of the resulting cells.

When, however, the eggs are held inclined more than 20°–30° the above rules do not hold good. Though even here the first cleavage seems to coincide with the plane of copulation of nuclei, yet these are often at right angles to the future median plane of the frog, though they may coincide with it in some cases. This is to be explained on the assumption that gravity acting upon yolk and nuclei determines a rotation of copulation direction.

Again in these much inclined eggs the lowest side of the black pole becomes the ventro-caudal part of the embryo, possibly because the formative yolk may accumulate there and influence the nuclear cleavage.

The most interesting of Roux's contributions appeared a year later.[9] In this he follows out the question of self-differentiation of the embryo, seeking to determine the amount and character of interaction of the part of an egg by destroying or injuring definite cells during cleavage. The eggs of *Rana esculenta* in the two celled stage were at first simply stabbed by a fine sharp needle, thrust into one cell, but as this did not produce much injury the needle was heated and often moved about inside the cell. Of such eggs about 20 per cent. developed only from the uninjured cell, others went to pieces or else developed normally. It is to be noted also that at this time of year, the latter part of the spawning season, some similar abnormalities were found in eggs that had not been operated upon at all. The various stages of abnormal growth were hardened, stained and sectioned. The results of such injury may be considered, first as relates to the uninjured and then to the injured half of the two celled stage.

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[9] V. Beiträge zur Entwicklungsmechanik des Embryo. Ueber die kunstliche Hervorbringung halber Embryonen durch Zerstörüng einer der beiden ersten Furchungs-kugeln, sowie über die Nachentwicklung der fehlenden Körper-hälfte. Virchow's Archiv., 114, pp. 113–153, 246–291. Pl. 2–3.

The single cell by side of the injured one develops in many cases into a half embryo, first a half blastula, a half gastrula then a half embryo with medullary fold, archenteron, chorda, mesoblast and metameres representing only half of the normal condition of these organs.

In the four-celled stage injury to both posterior cells sometimes resulted in formation of only anterior half of medullary folds. Injury to three or to one of the cells resulted either in one-fourth blastulæ or in the other cases three-fourths embryos. Finally injury above or below the first horizontal furrow gave rise to some cases of upper half blastulæ.

He concludes that as each of the first two cells may develop up to stage of medullary folds without aid from the other, there is marked self-differentiation and that the cleavage planes separate the material qualitatively and thus determine the subsequent position of the organs. The last experiment also indicates that the gastrula or embryo is a mosaic made up of at least four vertical elements or independent parts.

Turning now to the complex phenomena that take place in the cell operated upon, regarded by Roux as dead, though evidently this is scarcely justifiable from its subsequent history we find three series of events taking place: 1st disintegration, 2nd reorganization, 3d post generation.

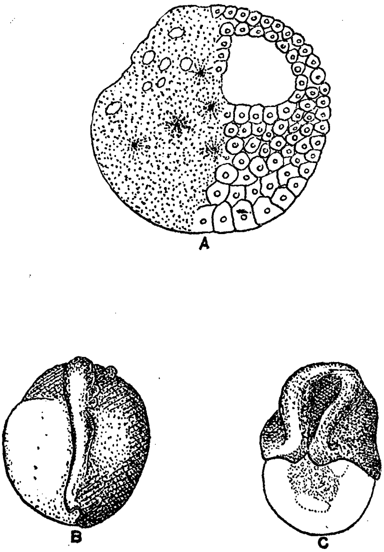
In the first category are included, a vacuolation of the yolk, the appearance of a net work within it in places and the formation of peculiar bodies regarded as nuclei derived from the original nucleus of the operated cell. Here again we must not overlook the fact that some eggs found at this season do not develop but have similar abnormal nuclei. Only about one-third of the eggs operated upon and subsequently sectioned present these phenomena of disintegration.

In all the operated eggs there are normal nuclei present in the half that was injured and these come in part from the original nuclei and in part by migration from the uninjured half, at least so the author concludes. These normal nuclei undergo further development and are associated with cell walls in the process of reorganization, the abnormal nuclei on the other hand collect in clusters and go to pieces. Where these abnormal nuclei and the vaculated nuclei are present reorganization of the yolk is delayed for some time but elsewhere the yolk presents rearrangement of its granules leading to the formation of cell walls. Besides the formation and arrangement of normal nuclei and the reconstruction of the yolk there is a third process in the reorganizations, namely the growth of cells from the uninjured half over the injured half or at least over such parts of it as present vaculated yolk. All three processes may take place at once or separately.

Post generation is the completion of the half of the embryo in which the above nuclear changes have regenerated the mass apparently killed by the injury of operation. It is externally manifested by the formation of a layer of pigmented cells over the operated half, the formation of the missing medullary fold which grows from before backward or of the posterior parts of both folds when we have an anterior half embryo. The complete tadpoles resulting are in part active, in part weak, easily killed creatures.

The internal changes that take place in this post generation as revealed by sections are the growth of a new ectoblast and mesoblast into the previously imperfect cellular mass by a process of successive rearrangement and differentiation of the yolk cells, adding themselves to the edges of the advancing layers in such wise as to form parts symmetrical with those in the uninjured half of the embryo. The entoblast also is formed from the free edge of the entoblast of the perfect half by rearrangement of yolk cells and there is no invagination, no gastrula nor blastula cavity formed in this newly forming half of the embryo. The germ layers thus form by a sort of regeneration from the interrupted surfaces of the old germ layers, but as the material comes from the new half of the embryo the old half may be regarded as exercising a sort of formative or assimilative action upon the irregular mass of yolk cells in the new half.

FIGURE I.



To recapitulate the chief results with the aid of fig. 1, A, B, C: A, being a half blastula resulting from injury of one of the first two cleavage cells and as yet not reorganized, seen in section: B, a right half larva from dorsal view and C are anterior-half larva. Injury to one of the first cleavage cells may result in the formation of a half embryo, to one of the first four to a fourth embryo, to three of the first four to a three-fourths embryo. The dead cells (regarded as dead by the author) may be revived and reorganized partly by division of the nucleus present and partly by inwandering of new nuclei and their division. The nucleation is followed by a cellulation and this by a regeneration of germ layers not following the normal course but growing out from the exposed surfaces of the layers already formed in the other half of the embryo. This definite process of post-generation seems due to the controlling action of the formed germ layers upon nuclei and yolk collected by chance in the places they occupy before being thus incorporated with the germ layers. Thus the reorganized parts are not capable of self differentiation as are the early cells in cleavage but are dependent upon influences coming from the other half of the egg or embryo.

An earlier paper by the same author, Roux,[1] has led to interesting facts and discussions regarding the axial relations of egg and embryo in the frog. In these experiments the eggs were put into semen for four minutes, then provided with a hair inserted into the gelatinous envelop as an index of movement and floated in a solution of gum arabic contained in a vessel of mercury that thus enabled one to see the reflected image of the under side of the egg. The eggs now take up a definite inclined position but subsequently, in 13 to 30 minutes change so as to stand vertically. Control experiments with eggs not fertilized show that the change in position does not take place as a rule. Hence fertilization is regarded as bringing about an alteration in the egg axes with reference to the lines of gravitation. The first cleavage plane would then pass through the egg in its secondary position which has been brought about by the entrance of the sperm. This led to the experiments previously reviewed, on the determination of the first plane by the plane of copulation of the nuclei.

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[1] W. Roux: II Beiträge zur Entwicklungsmechanik des Embryo. 3 Ueber die Bestimmung der Haupt-richtung des Froschembryo im Ei und die erste Theilung des Froscheies.

Breslauer arztliche Zeitschrift, 7, 1885. 1. nrs, 64–68, 73–77, 87–88, 100–101, 112–116, 125–128.

The validity of conclusions drawn from observations upon eggs in gum solutions is obviously, as Schultze has pointed out, very doubtful, especially when we find that of 47 eggs only 8 formed even the first cleavage plane and the inclination of these eight eggs in the gum was so obviously influenced by it, being 90°, 60°, 50°, 50°, 30°, 20°, 20°, 20°.

In another part of this paper it is found that frogs' eggs drawn out to double their normal diameter in narrow glass tubes assume a conical or else a lens shape, but cleave and at first transverse or at right angles to the tube, in the line of pressure. Again eggs in larger tubes wound about by wire through which an electric current was passing show no difference from the normal cleavage. The same is true when the eggs are between the poles of a magnet. Incidentally it was found that the eggs left in the tube did not continue development unless close to the air, at ends of tube or next bubbles, the position of organs formed or at least the gastrula mouth has, however, no reference to the side whence the air supply came.

With Pflüger, Roux finds the first cleavage plane is the median plane of the frog, yet not without exceptions since the normal sequence may be interrupted and the first plane actually found separate the anterior from the posterior part and thus represent the normal second plane. Rauber[2] it is to be noted, found somewhat similar irregularities. Thus in the frog the first plane in seven eggs made the following angles with the future median plane of the adult, 90°, 50°, 90, 85°, 0°, 82°, 90°. In the axolotl the same angles were, 80°, 53°, 90°, 50°, 90°, 30°, 90°, 2°, 90°, 90°, 70°, 80°, 32°, 90°, 90° in fifteen eggs observed.

Another point that appears to offer unusual difficulties to the experimentator is connected with the movement the egg performs after the embryo begins to form, which render the reference of organs to special regions of the egg by no means easy. Thus Roux[3, 4, 5] and Schultze working upon similar material by similar methods arrive at very different conceptions of the relationships of the dorsal and ventral parts of the frog to the white and black parts of the egg.

Roux holds that the medullary folds, that is, the dorsal region of frog, appear upon the white or lower pole. This is seen when eggs are fastened in normal positions and is also inferred from experiments in which injury to the black pole remains as injury to the ventral side of the embryo. The reason other observers find the dorsal area on the upper black pole is that the egg turns over so that the dorsal field floats uppermost. The blastopore first appears just beneath the union of black and white, the equator, and then shifts over while closing to the opposite side of the equator. Where the blastopore first appears arises the anterior end of the medullary plate and extends across the white pole to the closing region of blastopore. All this is on lower side when egg is fixed, but the free normal egg turns upward so that the region of first appearance of blastopore rises and carries the head area into the uppermost pole where the black pigment was at first.

(*To be continued.*)

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[2] A. Rauber: Furchung und Achsen-bildung. Zool. Ang. 9, 1886, p, 157–9.

[3] W. Roux: Zur ersten Entwicklung des braunen Grassfroches. O. Schultze, Biol. Centb. vii, 1888, pp. 421–424.

[4] W. Roux: Zur Frage des Axenbestimmung des Embryo im Froschei. Biol. Centb. viii, 1889, pp. 399–412.

[5] W. Roux: Ueber die Lagerung des Materiales des Medullarrohres im gefurchten Froschei. Anatomische Anzeiger iii, 1888, pp. 697–705, figs. 1–4.